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B. T. GALLOWAY, *Chief of Bureau.*

# FLORAL ABNORMALITIES IN MAIZE.

BY

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## LETTER OF TRANSMITTAL

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
*Washington, D. C., November 25, 1912.*

Sir: I have the honor to transmit herewith a paper entitled "Floral Abnormalities in Maize," by Mr. James H. Kempton, Assistant in Crop Acclimatization, and to recommend its publication as Bulletin No. 278 of the Bureau series.

Respectfully,

B. T. Galloway,
*Chief of Bureau.*

Hon. James Wilson,
*Secretary of Agriculture.*

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# FLORAL ABNORMALITIES IN MAIZE.

## INTRODUCTION.

Indian corn (*Zea mays*) belongs to a species which has no near relatives among either wild or cultivated plants. It has been under domestication for so long a period and has become so profoundly modified in structural characters that there is now much uncertainty as to its nearest affiliations. In its floral characters, particularly, the modifications have been so great that the structural analogies with other grasses have remained rather obscure. This is particularly true with respect to the pistillate inflorescence.

The study of abnormal forms and displaced parts is one of the best methods of tracing the evolutionary history of a plant. In *Zea mays* abnormal forms are of common occurrence, and it is seldom indeed that several distinct abnormalities are not found when even a few plants are carefully examined. They occur most frequently in varieties that have had little or no selection, probably because most abnormalities are in the nature of undesirable reversions and so have been suppressed in well-bred strains as the result of selection. They can be brought into expression again by inbreeding or by crosses between widely different types.

## NORMAL INFLORESCENCE.

The following brief description of the normal inflorescence in maize will serve as a basis for indicating more clearly the nature of the structural abnormalities to be described in detail.

The spikelets of the staminate inflorescence occur in pairs, of which one spikelet is sessile and the other is stalked, except in *Zea hirta*, where there usually are six spikelets borne together, and all are sessile. Each spikelet bears two flowers, each of which is provided with a glume, a lemma, a palea, a lodicule, and three versatile 2-celled stamens.

The spikelets of the pistillate inflorescence are also borne in pairs, but on relatively short pedicels of nearly equal length, each pair being located in an alveolus. The paired spikelets are ordinarily

arranged in double longitudinal rows, the adjoining pairs alternating with each other. (Fig. 1.) At least one variety of sweet corn, and frequently individuals of all varieties, show exceptions to this rowed arrangement of the spikelets. In these exceptions the spikelets are arranged indiscriminately, bearing seeds usually of the "shoe-peg" type.

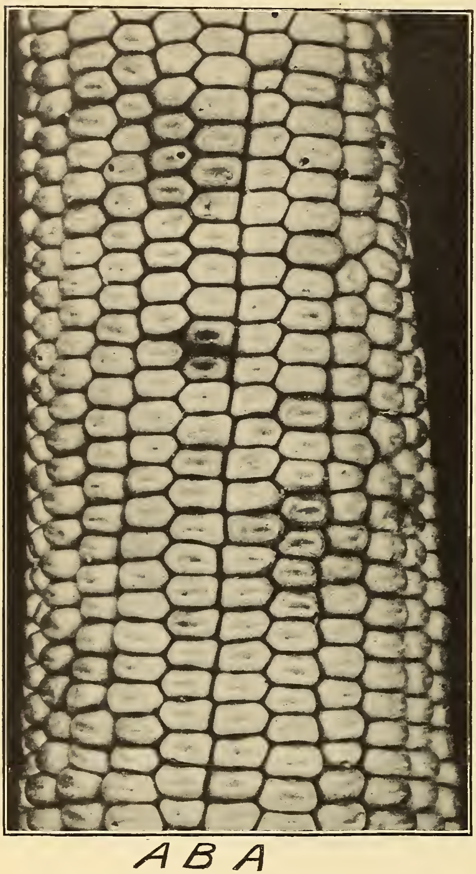



Fig. 1.—Section of an ear of maize, showing the arrangement of seeds. The straight line *B* is the division between opposite seeds representing the same pair of spikelets. The zigzag lines *A A* show the alternation between double rows of seeds that represent paired spikelets.

Unlike the staminate spikelet, the pistillate spikelet normally bears but one flower, the ovary of the second flower being completely aborted. The fertile flower develops into a seed of which the embryo is borne on the side toward the apex of the inflorescence. Like the staminate flower, each pistillate flower has a glume, a lemma, and a palea, but the lodicule, if it occurs, has never been observed. The bracts are much reduced in size in all except the pod corn (*Zea tunicata*), where they are greatly enlarged and entirely surround each seed.

The abortion of one of the flowers of the pistillate spikelet does not affect the development of its normal equipment of bracts. Consequently each seed is apparently equipped with six bracts, though as a matter of fact three of these bracts properly belong to the aborted flower.

## ABNORMAL PISTILLATE SPIKELETS.

In a variety of corn grown by the Hopi Indians in Arizona it was observed by Mr. G. N. Collins that some of the kernels on the ear were apparently inverted; that is, instead of bearing the embryo on

the side of the kernel toward the apex of the cob it was borne on the side toward the base. It was first assumed that this inversion was due to a crowding of the kernels on the ear. Since then, however, a similar phenomenon has been observed in several other cases, one of which was in *Zea tunicata.* The dissection of an ear of this latter type suggested the true explanation. In this ear it was observed that in several instances both of the ovaries in a spikelet had developed into seeds. (See Pls. I and II.)

In these cases the kernels were always found back to back, with the inverted kernel always coming from the lower flower. This discovery on the ear of pod corn suggested that this was also the explanation of the other cases of inverted seeds which had not been dissected, owing to the difficulty of removing the spikelets entire. A few dissections of the inverted seeds in the Hopi variety were obtained on further trial, which showed in nearly every case that the spikelets had developed seeds from both flowers, the seeds from the lower flower being inverted.

In all the examples in which one inverted seed was found alone in the spikelet traces of the upper flower could be seen, showing that the inverted seed developed from the lower flower, the upper one being aborted.

In a large number of instances this development, two kernels on one spikelet, was accompanied by the abortion of both flowers of the other spikelet of the pair. This, however, was not always the case, as a few examples were found with two kernels in one spikelet and one in the other, and one case where all four flowers of the paired spikelets produced seed. (See Pl. II.) The kernels were usually of the same size, though cases were noticed where the seed from the lower flower was smaller. Both seeds germinate equally well and produce seedlings of nearly the same vigor.

The ear of *Zea tunicata* with inverted seeds was found among the ears harvested from a planting made in 1911. This ear had been fertilized with pollen from the Hopi variety. In a careful examination of 25 original ears grown by the Hopi Indians of Arizona 6 were found with inverted seeds. A single inverted seed was also found in an ear of a complex hybrid made up of varieties from China, Salvador, and Mexico. The greatest number of inverted seeds or 2-flowered spikelets found on any one of these ears was three, on one of the ears of the Hopi variety. In 1912 the ear of *Zea tunicata* that had been hybridized with the Hopi variety was planted to observe the frequency of the occurrence of the 2-flowered female spikelets. A critical examination of the 16 ears resulting from this planting failed to reveal any inverted seeds.

## ABNORMAL STAMINATE SPIKELETS.

It was observed that among the plants there were several having a few female flowers in the male inflorescence. In these cases the ovary was produced in the upper flower of the sessile spikelet, the lower flower of this spikelet, as well as both flowers of the pediceled spikelet, remaining staminate. Most of the flowers which bore ovaries were perfect or nearly so, though the stamens were sometimes fewer than the normal number and were often sterile.

In all the cases observed where the stamens were fertile they were always three in number. Fertile stamens were never found in a flower having any sterile stamens; a flower either had fertile or sterile stamens, never both, and where fertile they were always of the normal number, three.

A few tassels bore on the lateral branches spikelets having two ovaries, one from each of the flowers. These were always in the sessile spikelet, the pediceled spikelet having both flowers staminate. This fact seems to indicate that the aborted spikelet which was found on the ear where two seeds had developed in the other spikelet of the pair probably corresponds to the pediceled spikelet of the pair.

Iltis[1] has observed that the sessile spikelet in the staminate inflorescence of maize is the first to change in sex, but he does not go farther and state which flower of this spikelet is the first to undergo the change. The fact that the seeds developed from the lower flower are always inverted seems to indicate that it is the upper flower of the spikelet which normally changes sex first. The change would then take place in the upper flower of the sessile spikelet first, followed by the upper flower of the pediceled spikelet, then the lower flower of the sessile spikelet, and lastly the lower flower of the pediceled spikelet.

The sessile spikelets having two ovaries also had stamens, usually one or two, and rarely three, in each flower, but these were never fertile. Only a few of these 2-flowered female spikelets produced seeds, though all were well pollinated artificially. These seeds were always back to back, both germs facing out, though they were not borne longitudinally with respect to the rachis, one with the germ toward the tip and the other with the germ toward the base, as is the case where they are found on the ear.

## INVERSION OF SEEDS ON THE EAR.

Included in the planting of experimental corn in 1912 were two rows of *Zea tunicata*. One row was from the same lot of seed which had in 1911 produced the one ear having inverted seeds. The other

[1] Iltis, Hugo. Ueber einige bei Zea mays L. beobachtete Atavismen. Zeitschrift für Induktive Abstammungs- und Vererbungslehre, Bd. 5, 1911, p. 38–57.

row was from an ear of another strain that had been self-pollinated in 1911. None of the 16 ears of this latter strain grown in 1911 showed inverted seeds, nor did the original ear.

The seed from the strain that in 1911 produced the ear with inverted seeds had in 1912 tassels with a few inverted seeds, but showed no inverted seeds in the 30 ears that were produced.

The row from the self-fertilized ear of the other strain produced 30 plants, of which 8 had ears with inverted seeds, or 2-flowered spikelets. (See Pl. II.) Four ears were dissected and counts made of the number of 1-flowered and 2-flowered spikelets, the results being shown in Table I.

TABLE I.—*Number of female spikelets with one and two flowers.*

| Plant No. | One flower. | Two flowers. |
|---|---|---|
| 1 | 534 | 23 |
| 2 | 495 | 16 |
| 3 (ear 1) | 471 | 10 |
| 3 (ear 2) | 524 | 48 |

In three of these ears almost all of the 2-flowered spikelets were found within 10 centimeters of the tip of the ear. On the second ear of plant 3, however, the 2-flowered spikelets were well distributed throughout the entire ear.

The tendency for the ears of maize to bear a staminate spike is a well-known phenomenon. The occurrence of 2-flowered spikelets near the apex and the tendency for an ear to have a staminate spike may be taken as a general indication that the tip is less completely specialized. The fact that the second ear had more 2-flowered spikelets, as well as a more even distribution over the ear, is also in accordance with this view, as the ears tend to become more like branches with staminate tips as they near the base of the plant and are therefore more likely to vary in floral structure. Unfortunately, there was only the one 2-eared plant that had 2-flowered spikelets on the ears, so it was impossible to ascertain whether the behavior of the second or lower ear on plant 3 was merely due to chance or was of regular occurrence.

When the spikelets of the male inflorescence produce female flowers, a greater proportion of these spikelets produce two flowers than of those on the pistillate inflorescence. This would account for the occurrence toward the tips of the ears of more 2-flowered spikelets as the tips tend to become staminate, although staminate tips have never been found in pod corn.

## OCCURRENCE OF SEEDS IN THE TASSEL OF POD CORN.

Several of the plants in the same row that produced the ears with 2-flowered spikelets also had greatly enlarged tassels which bore a large number of pistillate flowers. These plants produced no ears, but instead bore all their seeds in the tassel. Three of these tassels were dissected and counts made of the 1-flowered and 2-flowered female spikelets. It will be noticed that these tassels produced fully as many seeds as a fair-sized ear. The counts are shown in Table II.

TABLE II.—*Number of staminate spikelets with one and two pistillate flowers.*

| Tassel No. | One flower. | Two flowers. |
|---|---|---|
| 1 | 477 | 95 |
| 2 | 828 | 49 |
| 3 | 468 | 122 |

In tassel 1 there was one spikelet that had three well-developed seeds. This spikelet had the normal number of glumes, lemmas, and paleæ. This would seem to indicate that it was not a combination of two spikelets, as has been noticed in the staminate flowers where the number of glumes, lemmas, and paleæ are often more than the normal number. A tendency for the spikelets to become many flowered has often been noticed in the staminate flowers, where as many as 15 stamens have been found in one spikelet, the normal number being 6.

## CONNATE SEEDS.

Another fact connected with the normally aborted ovary is that in many cases other than pod corn, when both seeds from the same spikelet develop, they are united back to back, making what resembles one seed with two germs on opposite sides. These connate seeds would be regarded as 2-seeded fruits if a strict botanical interpretation were given their structure, for they are inclosed in a single pericarp. The seed coat proper remains separate and only partially surrounds the individual seeds, penetrating the place of union for only a short distance and then disappearing completely. The corneous layer, which surrounds an amylaceous interior in most seeds of the dent type, only partially surrounds the amylaceous portion of these connate seeds. This amylaceous interior of the connate seeds is without any line of demarcation. (Fig. 2.)

The connate seeds are usually about twice the size of the single seeds on the same ear, though sometimes the seed developed from the lower flower is smaller. Unfortunately there were not enough connate seeds to determine the difference in weight between these and single seeds. The two halves germinated at about the same time and

produced seedlings of equal vigor. Here, too, the number of seeds available for the germination test was too small to determine definitely whether the seeds always germinate at the same time and have equal vigor.

The union of the seeds which develop from the 2-flowered spikelets appears to take place very early, since it is to be observed that the two styles or silks are usually united. (Pl. I, fig. 5.)

There have been no cases observed of two maize seeds growing together except where both have been produced by one spikelet. In pod corn the seeds produced in 2-flowered spikelets are never united, owing perhaps to the larger and earlier development of the bracts which surround each seed.

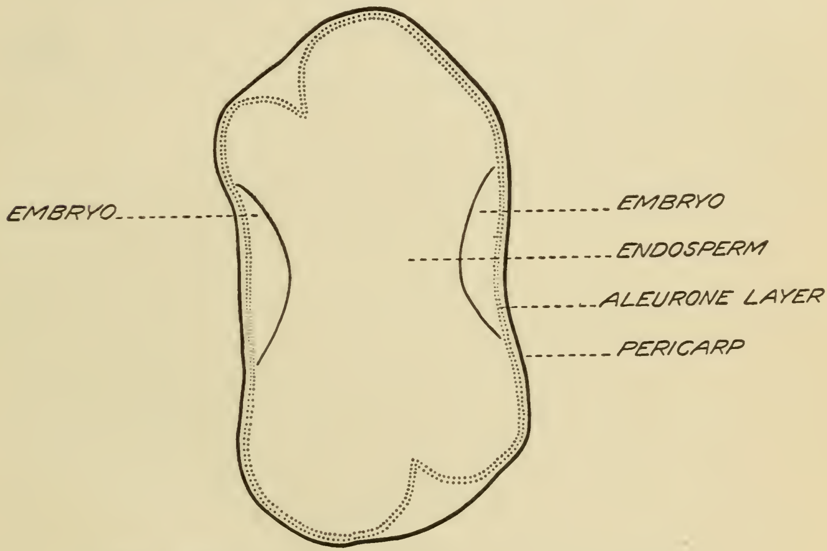



FIG. 2.—Diagram of a cross section of two connate maize seeds.

A large number of the seeds produced from 2-flowered spikelets in the Hopi variety were of the connate type, as were several from a Hopi × Mexican × Chinese hybrid. The union of the seeds was sometimes very striking when the two seeds differed in the color of the aleurone layer.

## POLYEMBRYONY.

The connate kernels are an entirely distinct phenomenon from kernels with double embryos, two of which have been found by Mr. W. L. Goss, who has charge of the germination work of the Seed Laboratory of the United States Department of Agriculture. In these cases the kernels were of normal size and shape, but had exceptionally large germs, which produced two vigorous seedlings. The seeds with double embryos were not dissected, but were planted

in the greenhouse, as they were found in January. They were destroyed by worms between Saturday night and Monday morning, when the greenhouses were without care. Mr. Goss has found only two of these seeds in the many thousands he has germinated. There was no appreciable difference between the two seedlings, as will be seen in Plate I, figure 3.

### EVOLUTIONARY SIGNIFICANCE OF ABNORMALITIES.

The origin of *Zea mays* is uncertain. It is believed by some botanists to have developed from an extinct group of grasses, while others believe it to be developed from a well-known group. It is within the limits of possibility that there are as yet undiscovered types able to multiply themselves and to exist in the wild state that are perhaps intermediate in form between Zea and its nearest known relative, Euchlaena. There can be little doubt that the varieties now commonly known would soon become extinct if left to reproduce themselves without the assistance of man.

We know that the aboriginal Americans grew corn with much less care than is now given to its culture, but with them it never reached its present efficiency in the yield of grain. It is evident that in increasing the efficiency of the maize plant the ability to hold its own in a wild state has been completely lost. It is not unreasonable to suppose that maize was much less difficult to grow 400 years ago, when the Europeans first began its culture. There probably is to be found among some of the isolated tribes of Indians in Mexico or Central America types of corn more nearly like the original wild plant upon which the first Indian culture was based. The methods of culture used by these isolated tribes have probably remained unchanged, though better forms may have arisen by unconscious selection and modified their primitive types.

The tendency of evolution is toward complicated types with more highly specialized parts. Sudden and abnormal changes are usually looked upon as reversions, while the development of new characters is attributed to the slower method of selection. Accepting this view, the frequent development of 2-flowered female spikelets on the pistillate inflorescence of *Zea mays* has a significant bearing on its uncertain evolution.

There is a striking resemblance in vegetative characters between *Zea mays* and certain members of the Andropogoneæ, but the normal floral parts are very different in structure and location. From the common abnormalities and variations in the floral organs of maize a continuous series can be arranged connecting the Maydeæ and Andropogoneæ.

The chief floral difference between the Maydeæ and the Andropogoneæ is that the Andropogoneæ normally have androgynous

flowers, while the flowers of the Maydeæ are usually unisexual. This difference, which has been used to divide the two tribes, is not fundamental as far as *Zea mays* is concerned. One species, *Zea tunicata*, commonly has plants that bear a terminal inflorescence composed of spikelets, a large percentage of which are perfect flowered. In other species of Zea adverse external conditions often result in androgynous flowers being produced in the male inflorescence. The character, which environment changes so essentially in form and which appears as a normal character in some of the plants of *Zea tunicata*, can hardly serve to keep *Zea mays* and some members of the Andropogoneæ separated.

Neither Euchlaena nor Tripsacum normally have 2-flowered female spikelets, though in both of these the male spikelets are 2-flowered, as in *Zea mays*. The examination of a large number of ears resulting from hybridizing Euchlaena and Zea revealed one inverted seed. In this case the upper flower of this spikelet was aborted, though traces of it could be seen.

From the fact that neither Euchlaena nor Tripsacum have 2-flowered female spikelets, we are led back into the Andropogoneæ, where the next nearest relatives are found.

Haeckel, Goebel, and others have called attention to the close resemblance of *Zea mays* to certain members of the Andropogoneæ, chiefly on account of the frequent occurrence of androgynous flowers. The occurrence of 2-flowered female spikelets on the pistillate and staminate inflorescence, while less frequent than the occurrence of androgynous flowers, would seem to be of equal importance in strengthening the relation of *Zea mays* to the Andropogoneæ.

## CONCLUSIONS.

Inverted seeds have been found on the male and female inflorescences of maize.

These inverted seeds are developed from the lower flower of the spikelet, which is normally aborted.

Flowers having ovaries and stamens always had the normal number, three, if the stamens were fertile.

Flowers having both ovaries and sterile stamens often had less than three stamens. Fertile and sterile stamens were never found in the same flower.

Spikelets with two ovaries never had any fertile stamens, but sometimes had from one to three sterile stamens.

The occurrence of a larger percentage of 2-flowered spikelets near the tip of the female inflorescence may be taken to indicate that the tip of the ear is less highly specialized than the remainder of the ear.

That there is a well-defined tendency for both male and female spikelets to become many flowered is evidenced by the fact that one

spikelet has been found with three seeds, and male spikelets with many more than the normal number of stamens are of common occurrence.

The development of two ovaries in one spikelet is not definitely correlated with the abortion of the other spikelet of the pair. A few cases have been found where four seeds have developed from the two spikelets of a pair and many pairs that have produced three seeds.

The development of two ovaries in one spikelet must be simultaneous, as a large number of cases have been found where the two seeds from one spikelet have grown together with a single pericarp. These connate seeds had been fertilized through a double silk which was attached to the pericarp near the union of the two seeds.

Connate seeds are a distinct phenomenon from single seeds with a double embryo, two of which have been seen.

The development of 2-flowered female spikelets is looked upon as a reversion to a more primitive type, the tendency of evolution being toward more complicated types with more highly specialized parts.

Neither Euchlaena nor Tripsacum, the two nearest known relatives of *Zea mays*, have 2-flowered female spikelets, and the occurrence of this character in maize is held to strengthen the relationship between Zea and the Andropogoneæ, already indicated by the occurrence of androgynous flowers.

# PLATES.

## DESCRIPTION OF PLATES.

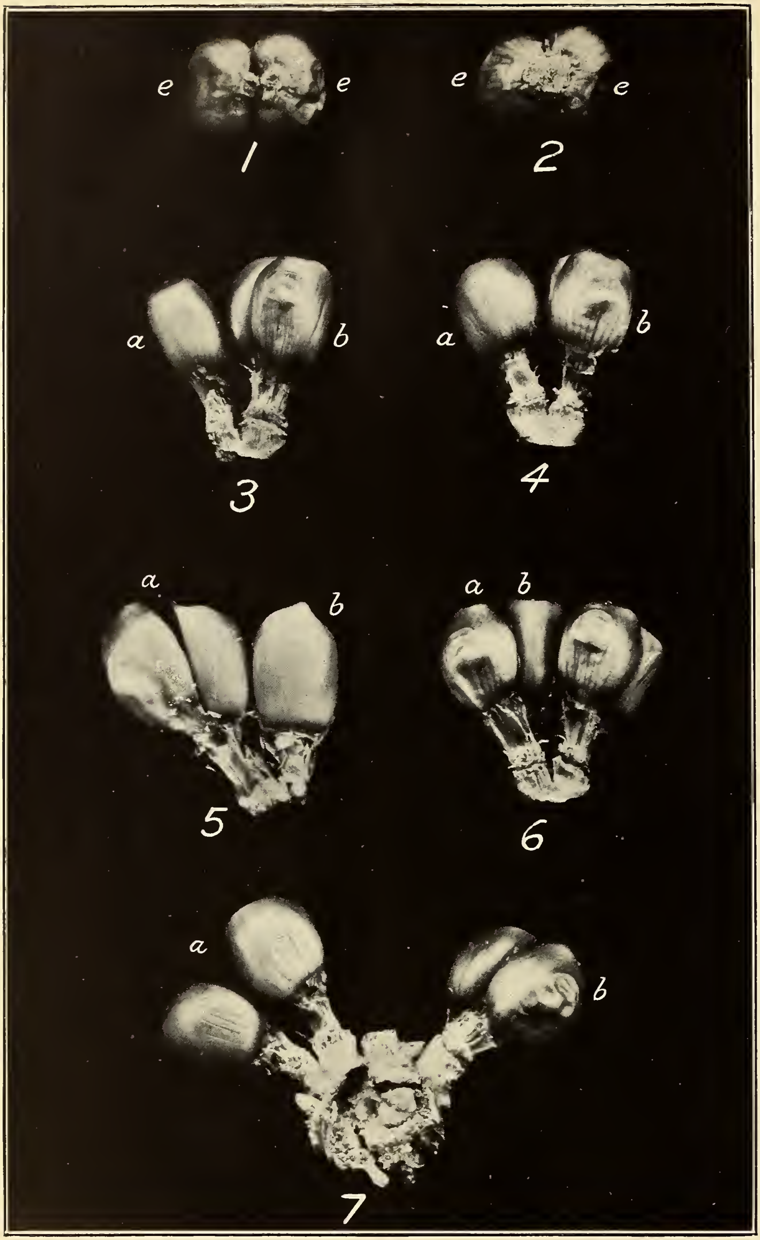
PLATE I. Fig. 1.—Two seeds from a single spikelet showing equal development of the young seedlings. Fig. 2.—Germinated connate seeds showing equally developed seedlings from both germs. Fig. 3.—A polyembryonic seed from a commercial variety of maize. Fig. 4.—Paired spikelets from an ear of maize. It will be observed that one spikelet has remained sessile and pistillate, while the second spikelet has become pediceled and staminate. Fig. 5.—A group of connate seeds from an ear of the Hopi variety of maize. The ear from which these seeds were taken was grown by the Indians on their reservation in Arizona. In the center of the left-hand connate seeds, in the middle row, the place where the fasciated silk was attached is plainly visible. The pollen tubes which fertilized the two embryos must both have entered at this point. One half of these connate seeds was a bright yellow, while the other was a deep blue. It will be noticed that the division between the two members of these connate seeds is always diagonal.

PLATE II.—A group of seeds from an ear of pod corn (*Zea tunicata*). The four seeds in the upper row are from two spikelets. The embryos, it will be observed, are on opposite sides. The six seeds in the second row are from four spikelets. The two seeds on one stalk in each group are from one spikelet. The single seed on a stalk is from the other spikelet of the pair. This is also true of the three left-hand seeds in the third row from the top. The four seeds on the right hand of the third row from the top have developed from two paired spikelets, showing that the development of the lower flower into a seed is not always accompanied by the abortion of any of the flowers, though one spikelet of the pair is often aborted. The figure at the bottom shows a section of the cob with all but four seeds removed. The two seeds at the left are from spikelets, each on a separate stalk. The other two seeds at the right are both on one pedicel and one is inverted. These seeds both came from one spikelet and represent the upper and lower flowers. The seed on which the embryo is visible is from the lower flower.






FIG. 1.—TWO SEEDS FROM A SINGLE MAIZE SPIKELET. (NATURAL SIZE.) FIG. 2.—GERMINATED CONNATE SEEDS. (NATURAL SIZE.) FIG. 3.—A SEED WITH TWO EMBRYOS. (NATURAL SIZE.) FIG. 4.—PAIRED MALE AND FEMALE SPIKELETS FROM AN EAR OF MAIZE. (ENLARGED 1½ DIAMETERS.) FIG. 5.—CONNATE SEEDS IN THE HOPI VARIETY OF MAIZE; *e* INDICATES POSITION OF EMBRYO. (ENLARGED 1½ DIAMETERS.)




SEEDS FROM AN EAR OF ZEA TUNICATA.

Figs. 1 and 2.—Pairs of seeds each from a single spikelet; *e*, indicates position of embryos. Figs. 3 and 4.—*a*, One seed from a spikelet with germ toward apex of ear; *b*, two seeds from a spikelet with embryos on opposite sides. Fig. 5.—*a*, Two seeds from a single spikelet, both on one pedicel; *b*, a single seed from one spikelet. Fig. 6.—Paired spikelets which have each developed two seeds. *a*, Inverted seed developed from lower flower; *b*, seed developed from upper flower. Fig. 7.—Section of cob. *a*, Normal development of seeds from a pair of spikelets, each on a separate pedicel; *b*, two seeds from a single spikelet, both on a single pedicel. (Enlarged about $1\frac{1}{2}$ diameters.)